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The monophyly of Protorosauria (Reptilia, Archosauromorpha): a preliminary analysis

Abstract – This paper presents a preliminary analysis of protorosaur interrelationships based on the combination of the data published by Benton & Allen (1997), Jalil (1997), and Dilkes (1998). As was found in previous analyses by these authors, protorosaurs yield low resolution under parsimony analysis because of a high percentage of missing data in some taxa. *Kadimakara*, *Malerisaurus langstoni*, and *Trachelosaurus* are the most problematical taxa in that respect. Their deletion from the analysis dramatically improved resolution in a strict consensus tree. The analyses here presented confirm the result obtained by Dilkes (1998) that showed the protorosaurs as conventionally conceived to be paraphyletic. *Prolacerta* is more closely related to *Proterosuchus* and *Euparkeria* than to the other taxa conventionally included in protorosaurs (in one data combination, *Protorosaurus* joined *Prolacerta*, *Proterosuchus* and *Euparkeria*). *Macrocnemus*, *Langobardisaurus*, *Tanystropheus* and *Tanytrachelos* form a well-confirmed clade that may include the enigmatic *Cosesaurus*. In various data combinations *Drepanosaurus* and *Megalancosaurus* were found to be either related to (in a basal polytomy), or nested within protorosaurs. In either case, *Drepanosaurus* and *Megalancosaurus* were found to be more closely related to one another than to other protorosaurs, and as a group they were in some searches found to be more closely related to the *Macrocnemus* – *Langobardisaurus* – tanystropheid clade than to *Protorosaurus* or *Prolacerta*. The position of *Jesairosaurus* within the Protorosauria remains unresolved, although in one search the genus grouped with *Drepanosaurus* and *Megalancosaurus* in an unresolved trichotomy. Future analysis of protorosaur interrelationships based on the original material will not only have to address the problem of missing data, but also problems of character analysis and coding.

Key words: Protorosauria, Prolacertiformes, reduced strict consensus, phylogenetic analysis.

Riassunto – Monofilia dei protorosauri (Reptilia, Archosauromorpha): un'analisi preliminare.

Vengono presentati i risultati di un'analisi preliminare delle relazioni filogenetiche tra i taxa tradizionalmente inclusi nel gruppo Protorosauria. Tale analisi si basa su un set di dati ottenuto combinando quelli pubblicati da Benton & Allen (1997), Jalil (1997) e Dilkes (1998). Come già evidenziato da detti autori, con un'analisi filogenetica condotta con il metodo della parsimonia, le relazioni all'interno del gruppo restano praticamente irrisolte, a causa dell'elevato numero di dati mancanti in

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alcuni taxa (in particolare: *Kadimakara*, *Malerisaurus langstoni* e *Trachelosaurus*). Escludendo dall'analisi tali *taxa*, le relazioni tra gli altri protorosauri appaiono decisamente più definite, come si può evincere dall'elevato grado di risoluzione dello *strict consensus tree* ottenuto. L'analisi qui presentata concorda con il risultato ottenuto da Dilkes (1998), giungendo alla conclusione che il taxon Protorosauria, così come tradizionalmente concepito, rappresenta un gruppo parafiletico: il genere *Prolacerta* risulta infatti imparentato più strettamente con *Proterosuchus* ed *Euparkeria* di quanto lo sia con i taxa tradizionalmente considerati ad esso più affini inclusi nei protorosauri (in uno dei cladogrammi ottenuti *Protorosaurus* risulta il *sister-group* di *Prolacerta*, *Proterosuchus* ed *Euparkeria*). *Macrocnemus*, *Langobardisaurus*, *Tanystropheus* e *Tanytrachelos* costituiscono un clado ben supportato dai dati, nel quale potrebbe essere eventualmente incluso l'enigmatico genere *Cosesaurus*. *Drepanosaurus* e *Megalancosaurus* risultano invariabilmente imparentati (in una politomia basale) con i protorosauri o all'interno del gruppo stesso. In ambedue i casi, da un punto di vista filogenetico, *Drepanosaurus* e *Megalancosaurus* sono più affini l'uno all'altro di quanto lo siano ad altri protorosauri e, come gruppo nel loro insieme, risultano in alcuni casi più affini al clado *Macrocnemus* – *Langobardisaurus* – tanistrofeidi che a *Protorosaurus* o *Prolacerta*. La posizione di *Jesairosaurus* all'interno dei protorosauri rimane poco chiara, sebbene in un caso il genere sia associato a *Drepanosaurus* e *Megalancosaurus* in una tricotomia irrisolta. Una futura approfondita analisi delle relazioni filogenetiche dei protorosauri implica il riesame diretto dei materiali, volto a risolvere, almeno in parte, il problema dei dati mancanti e i dubbi relativi all'interpretazione e alla codificazione di alcuni dei caratteri utilizzati in letteratura.

Parole chiave: Protorosauria, Prolacertiformes, *reduced strict consensus*, analisi filogenetica.

Introduction

The protorosaurs, also sometimes referred to as prolacertiforms (Chatterjee, 1986, established the priority of Protorosauria Huxley, 1871 over Prolacertiformes), are an important radiation of terrestrial and aquatic Triassic reptiles with a wide geographic distribution. *Protorosaurus*, from the early Late Permian (*Kupferschiefer*) of Germany, is the earliest representative of the protorosaur clade. Interest in the group increased after Parrington (1935) suggested that *Prolacerta broomi* from the Lower Triassic (*Lystrosaurus Zone*) of South Africa was ancestral to modern "lizards". He demonstrated that the latter had a diapsid skull modified by the reduction of the lower temporal arch. Since then, protorosaurs, such as *Prolacerta*, *Macrocnemus*, and *Tanystropheus*, have played an important role in discussions of the origin of extant squamates (e.g. Peyer, 1931a, 1937; Kuhn-Schnyder, 1954, 1974 [opposed by Romer, 1966, 1968]; and Wild, 1973, 1976, 1980a [opposed by Evans, 1988]). However, Gow (1975) was the first to question the protorosaur-squamate relationship. Instead, he hypothesized archosaur affinities of *Prolacerta*. This view has since been repeatedly supported by cladistic analyses (e.g., Benton, 1985; Evans, 1988). As the protorosaur radiation became more completely known (assimilating, *inter alia*, what had been thought to be a Triassic bird ancestor: Sanz & López-Martínez, 1984), knowledge of their phylogenetic interrelationships became more refined (e.g. Benton & Allen, 1997; Jalil, 1997). More recently the drepanosaurids have also been associated with the protorosaur radiation (Benton & Allen, 1997; Dilkes, 1998).

The family Drepanosauridae was erected by Olsen & Sues (1986) to include *Drepanosaurus unguicaudatus* (Pinna, 1980, 1984, 1986; Renesto, 1994a; Renesto & Paganoni, 1995) and *Megalancosaurus preonensis* (Calzavara, Muscio & Wild, 1981; Renesto, 1994b, 2000; for a summary statement see Pinna, 1993), enigmatic archosauromorphs with arboreal adaptations (for arboreal adaptations of *Drepanosaurus* see Renesto, 1994a) from the Upper Triassic (Norian) of northern Italy. Pinna (1980, 1987) identified three specimens as immature specimens of

Drepanosaurus that were later recognized as specimens of *Megalancosaurus* by Renesto (1994a: 249, 1994b: 38): so, *Drepanosaurus* is actually known from the holotype only (Pinna, 1980, 1984, 1986; Renesto, 1994a), which is a well-preserved skeleton that lacks the head and neck, and from a possible juvenile, tentatively ascribed to the same genus (Renesto & Paganoni, 1995). The family Drepanosauridae now also includes *Dolabrosaurus aquatilis* (Berman & Reisz, 1992) and *Hypuronector* (Colbert & Olsen, 2001) from the Upper Triassic (Carnian) of the United States, described as aquatic forms.

Both Benton & Allen (1997) and Jalil (1997) noted problems in the analysis of the phylogenetic relationships of protorosaurs caused by very incompletely known taxa. Jalil (1997) identified *Kadimakara* (Bartholomai, 1979), *Malutinisuchus* (Otschev, 1986), *Prolacertoides* (Young, 1973), and *Trachelosaurus* (Broili & Fischer, 1917) as the main culprits. Evans (1988) cautions that the two partial skulls that have been assigned to *Kadimakara* (Bartholomai, 1979) may not even belong to the same animal. *Malutinisuchus* (Otschev, 1986) is known only from very few bone fragments that include two fragments of limb bones (?humerus), two fragments of (probably) pectoral girdle elements, and an elongated cervical vertebra with a low neural spine (holotype) reminiscent of the prolacertiform condition (Jalil, 1997). Given the incompleteness of the specimen, we decided not to include it in the present analysis. The same is true for the holotype and only known specimen of *Prolacertoides*, which comprises the anterior part of a skull (Young, 1973; see also Sun *et al.*, 1992): we consider it, again, to be too incomplete to be included in this analysis. *Trachelosaurus* was considered a "primitive" sauropterygian by Broili & Fischer (1917). Huene (1944) hypothesized that Broili & Fischer (1917) were misled to classify *Trachelosaurus* as a sauropterygian by the high number of elongated cervical vertebrae, and concluded that the slab contains remains of two individuals of a taxon close to *Protorosaurus*. Based on Huene's (1944) observation, Romer (1956: 657) included *Trachelosaurus* in the Protorosauridae.

Two other problematical taxa are *Rhombopholis* and *Malerisaurus*. *Rhombopholis scutulata* (Owen, 1842) is a metataxon (no known autapomorphies), but shares protorosaur synapomorphies in vertebral structure (Benton & Walker, 1996).

With respect to the two species of *Malerisaurus* recognized by Chatterjee (1980, 1986), Evans (1988) found that the skulls of both are poorly preserved, and that Chatterjee's reconstructions are heavily based on *Prolacerta*. The postcranial material could be protorosaur, or some other small archosaur.

The interrelationships of protorosaurs

Wild (1980a, fig. 13) summarized the conventional view of "prolacertiform" interrelationships that prevailed at that time: the "Prolacertiformes" and the Eolacertilia form the two main branches of the Lacertilia, which are to be derived from eosuchians. *Protorosaurus* lies at the eosuchian root of the "Prolacertiformes": *Prolacerta* is the common ancestor of two "prolacertiform" clades, one comprising *Macrocnemus*, the other comprising the various species of *Tanystropheus*. In a postscript, he accepted what was then the newly described *Tanytrachelos* (Olsen, 1979) as closely related to *Tanystropheus*, but rejected any positive statement on *Cosesaurus* on account of its difficult preservation.

Gauthier *et al.* (1988) included Protorosauria in their analysis without commenting on their composition. In contrast, Evans (1988) offered the first comprehensive analysis (not computer aided) of protorosaur interrelationships, including the genera *Boreopricea* (Tatarinov, 1978), *Cosesaurus* (Ellenberger & Villalta, 1974; see also Ellenberger, 1977, 1978), *Kadimakara* (Bartholomai, 1979), *Macrocnemus* (Nopcsa, 1930, 1931; Peyer, 1931b, 1937), *Malerisaurus* (Chatterjee, 1980, 1986), *Megalancosaurus* (Calzavara, Muscio & Wild, 1981), *Prolacerta* (Parrington, 1935), *Prolacertoides* (Young, 1973), *Protorosaurus* (Meyer, 1856), *Tanystropheus* (Meyer, 1847-1855; Wild, 1973, 1980a, b), *Tanytrachelos* (Olsen, 1979), and *Trachelosaurus* (Broili & Fischer, 1917). This is the composition of the Protorosauria that is generally accepted today, with the addition of *Langobardisaurus* (Bizzarini & Muscio, 1994; Renesto, 1994c; Renesto & Dalla Vecchia, 2000; Renesto, Dalla Vecchia & Peters, 2002), *Jesairosaurus* (Jalil, 1997) and, perhaps, all drepanosaurids (see Dilkes, 1998, and below). Evans (1988) discussed the arguments offered by Wild (1980a) in support of lepidosaur (squamate) relationships, but rejected them. In her analysis, she was unable to resolve the relationships of the poorly known genera *Kadimakara* (Bartholomai, 1979), *Malerisaurus* (Chatterjee, 1980, 1986), *Prolacertoides* (Young, 1973), and *Trachelosaurus* (Broili & Fischer, 1917), and she found *Protorosaurus* and *Prolacerta* to be part of a basal trichotomy with all other protorosaurs (her "gray area" at the base of the prolacertiform-archosaur dichotomy: Evans, 1988: 228). The latter formed the following hierarchy: (*Boreopricea* (*Macrocnemus* (*Cosesaurus* (*Tanystropheus*, *Tanytrachelos*)))). Evans (1988: 244) did reserve judgment on the position of *Megalancosaurus*, that she found to be the sister-group of the protorosaurs, suggesting that it "is an archosauromorph related to prolacertiforms and archosaurs.". Since her paper was published, more and better material of *Megalancosaurus* has been described (Renesto, 1994b; Renesto, 2000).

Computer supported cladistic analyses of protorosaur relationships were first conducted by Benton & Allen (1997) and Jalil (1997). Both studies comment on the problem of missing data and "rampant homoplasy". Benton & Allen's (1997) study reported the important signal of a possible paraphyly of the genus *Tanystropheus* and first recognized the protorosaur relationships of *Megalancosaurus*. *Megalancosaurus* nested within protorosaurs as sister taxon of *Protorosaurus* in a rather labile tree (that also included *Trilophosaurus* as sister-taxon of *Prolacertoides*).

Jalil (1997) obtained resolution of protorosaur relationships only by deletion of the poorly known taxa *Trachelosaurus*, *Prolacertoides*, *Malutinisuchus* and *Kadimakara*. *Protorosaurus* and *Prolacerta* again occupy a basal position; the deeply nested position of *Boreopricea* is unexpected. Otherwise, the deeply nested taxa are the same as in the previous studies, with some instability of the relative positions of *Langobardisaurus* and *Macrocnemus*. *Tanystropheus* (Wild, 1973, 1980a, b) was coded as single terminal, and the monophyly of the genus therefore was not tested.

Peters (2000) re-analyzed the data sets of Evans (1988) and Jalil (1997), but also added taxa such as *Drepanosaurus*, *Longisquama*, *Sharovipteryx*, *Preondactylus* and *Eudimorphodon*. *Drepanosaurus* and *Megalancosaurus* were found to be sister-taxa, placed in a basal trichotomy that includes the *Protorosaurus* – *Prolacerta* clade and the other protorosaurs (based on Evans, 1988). *Tanystropheus* (coded as single terminal) and *Tanytrachelos* were again found to be sister-taxa, and *Cosesaurus* as well as *Langobardisaurus* were found to be closer to that clade than to *Macrocnemus*. Peters proposed the heterodox hypothesis that protorosaurs (prolacertiforms) may be related to pterosaurs.

Finally, a very interesting analysis was presented by Dilkes (1998): while investigating basal archosauromorph relationships in general, he obtained the result of paraphyly of the protorosaurs (prolacertiforms). He again included *Drepanosaurus* in the analysis, and not surprisingly found it to group with *Megalancosaurus* inside the protorosaurs. *Prolacerta*, however, was not found to nest inside protorosaurs, but rather to be the sister-taxon of a *Proterosuchus* – *Euparkeria* clade, thus rendering the traditional Protorosauria (Prolacertiformes) paraphyletic. Leaving multistate characters unordered, the *Macrocnemus* – *Langobardisaurus* – *Tanystropheus* clade forms a trichotomy; ordering multistate characters shows *Langobardisaurus* closer to *Tanystropheus* than *Macrocnemus*.

For this paper we combined the data matrices of Benton & Allen (1997), Jalil (1997), and Dilkes (1998) in order to test protorosaur monophyly, and the relationships of *Drepanosaurus* and *Megalancosaurus*.

Re-analysis of previous work on protorosaur interrelationships

The data offered by Benton & Allen (1997) and by Jalil (1997) were combined for re-analysis. The data sets overlap, in part. The coding of Benton & Allen (1997, BA) was followed for the following characters that overlap with the data of Jalil (1997, J), which were correspondingly deleted: BA 2 – J 61; BA 5 – J 50; BA 9 – J 54; BA 11, 12 – J 27, 39, 43; BA 17, 18 – J 56; BA 20 – J 40; BA 22 – J 41; BA 24 – J 67; BA 25 – J 57; BA 26 – J 44; BA 27 – J 32; BA 29 – J 47; BA 30 – J 33, 51; BA 31 – J 46; BA 32 – J 55; BA 36 – J 22; BA 40 – J 59; BA 41 – J 35; BA 42 – J 53; BA 43 – J 58; BA 46 – J 12; BA 48 – J 60. The data matrix includes 95 characters, coded for *Petrolacosaurus* and *Youngina* (outgroup), and *Rhynchosaurus*, *Trilophosaurus*, *Drepanosaurus*, *Megalancosaurus*, *Protorosaurus*, *Boreopricea*, *Kadimakara*, *Malerisaurus langstoni*, *Malerisaurus robinsonae*, *Prolacerta*, *Trachelosaurus*, *Macrocnemus*, *Cosesaurus*, *Langobardisaurus*, *Tanystropheus longobardicus*, *Tanystropheus meridensis*, *Tanytrachelos*, *Jesairosaurus* (in-group). *Drepanosaurus*, which was not included by Benton & Allen (1997), and Jalil (1997), was coded by us for inclusion in our analysis on the basis of published descriptions. Benton & Allen's (1997) characters were coded for *Jesairosaurus* on the basis of Jalil's (1997) description. Benton & Allen (1997) coded both, *Malerisaurus langstoni* and *Malerisaurus robinsonae*, whereas Jalil (1997) did not differentiate between these two species in his coding. The data matrix offered by Jalil (1997) indicates that his codings for *Malerisaurus* are based on *M. langstoni*, to which we added the coding of *M. robinsonae* for Jalil's (1997) characters based on its published description. Again unlike Benton & Allen (1997), Jalil (1997) did not differentiate between the two species of *Tanystropheus*, viz. *T. longobardicus* and *T. meridensis*. We coded Jalil's (1997) characters for both species based on personal observation. The data matrix was analyzed using the heuristic search option (all characters equally weighted) in PAUP (Swofford, 1990; Swofford & Begle, 1993). The search was abandoned after 13,878 trees were retained (TL = 161), i.e., more trees than RadCon is able to read (see comments below). The strict consensus tree of those 13,878 trees yielded no resolution within the protorosaurs except for the pairing of *Tanystropheus longobardicus* with *Tanytrachelos*, but it did yield the monophyly of the protorosaurs as conventionally perceived.

Deleting the three taxa that are the most incompletely known (*Kadimakara*, *Malerisaurus langstoni*, *Trachelosaurus*) from the analysis yielded nine equally parsimonious trees (TL = 159, CI = 0.535, RI = 0.630) with some interesting results (Fig. 1):

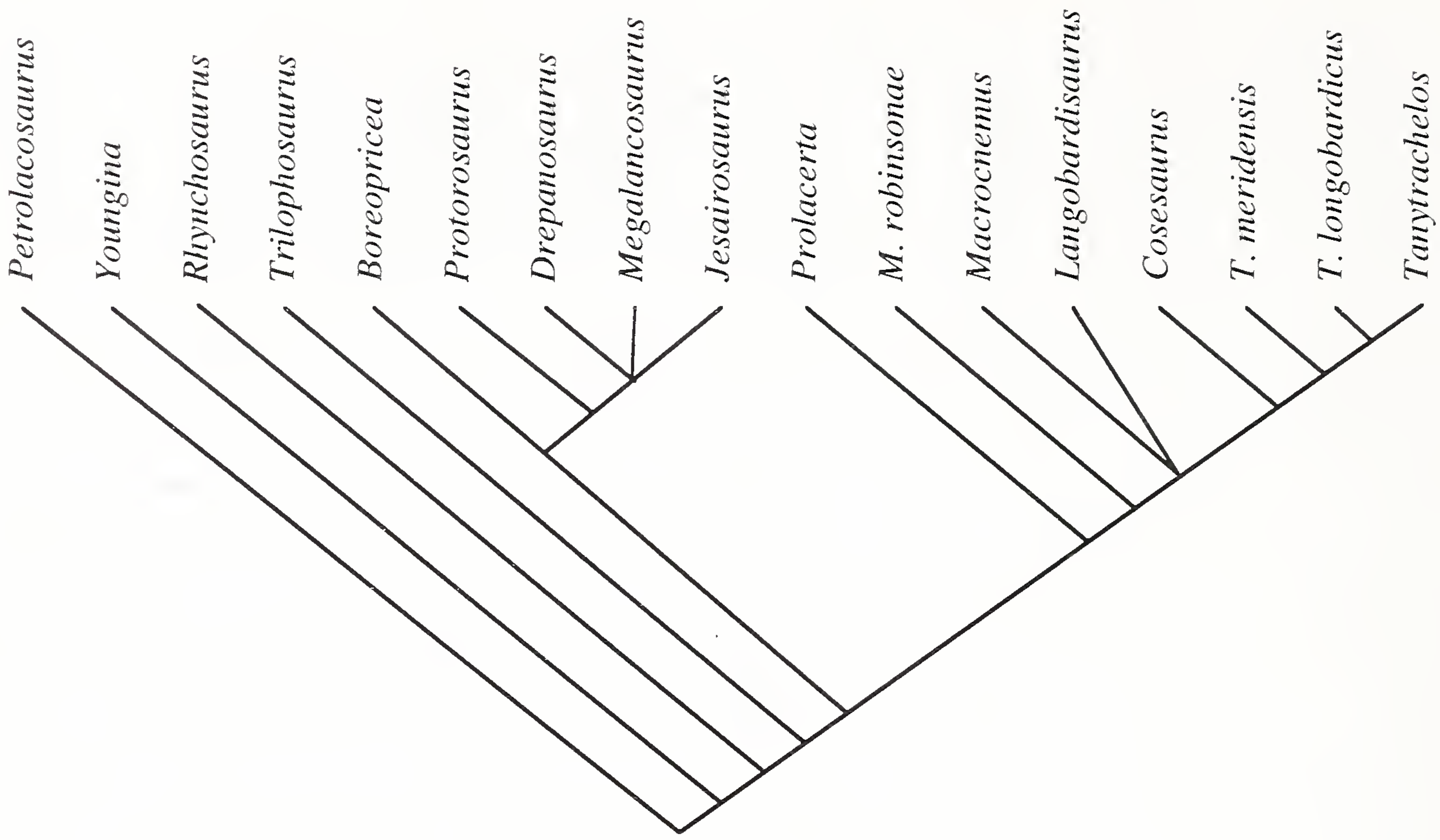

Fig. 1 – Protorosaur interrelationships based on the combined data from Benton & Allen (1997) and Jalil (1997). The incompletely known taxa *Kadimakara*, *Malerisaurus langstoni*, and *Trachelosaurus* are omitted.
Fig. 1 – Interrelazioni filogenetiche dei protorosauri risultanti dall'elaborazione dei dati ottenuti combinando quelli di Benton & Allen (1997) e di Jalil (1997). *Kadimakara*, *Malerisaurus langstoni* e *Trachelosaurus*, taxa poco conosciuti dal punto di vista anatomico, non sono stati presi in considerazione.

Interesting aspects of this result include the grouping of *Jesairosaurus* with *Drepanosaurus* and *Megalancosaurus* in an unresolved trichotomy with *Protorosaurus* and *Boreopricea* as successive sister-taxa to that trichotomy. *Prolacerta* and *Malerisaurus robinsonae* are successive sister-taxa to an unresolved trichotomy which includes *Macrocnemus*, *Langobardisaurus*, and a fully resolved clade that comprises (*Cosesaurus* (*Tanystropheus meridensis* (*Tanystropheus longobardicus*, *Tanytrachelos*))), and hence shows the genus *Tanystropheus* to be paraphyletic. Overall, protorosaurs would thus seem to include the enigmatic genera *Drepanosaurus* and *Megalancosaurus*. However, none of those nodes has a Bremer support index (Bremer, 1988) larger than 1 except the (*Macrocnemus*, *Langobardisaurus* (*Cosesaurus* (*Tanystropheus meridensis* (*Tanystropheus longobardicus*, *Tanytrachelos*)))) clade, which collapses after the addition of two steps to the original tree length.

We deleted *Kadimakara*, *Malerisaurus langstoni*, *Trachelosaurus* on the basis of anticipated problems that could be caused by the many missing data that cannot be coded for these taxa (thus coded as '?'; Kearney, 2002). We subsequently tested the validity of these deletions by a search for the reduced strict consensus tree(s) using the software package RadCon (Thorley & Page, 2000). Using the search option for reduced consensus analysis over the 10,000 of the 13,878 equally parsimonious trees that RadCon can read, RadCon will look for the "backbone" of the strict consensus tree, in the sense that it will find the sets of taxa that share the same relationships across all equally parsimonious tree. The results are a set of reduced consensus trees that successively exclude those taxa whose positions are unstable in all equally parsimonious trees. In the case of the 10,000 equally parsimonious trees obtained using the data set that combines the data from Benton & Allen (1997) and Jalil (1997), RadCon yielded eight reduced consensus trees, successively deleting a combination of various taxa. The taxa that were first deleted were *Kadimakara* and *Trachelosaurus*, but other taxa that were identified as of an unstable position by RadCon include *Malerisaurus langstoni* as well as *Cosesaurus*, *Jesairosaurus*, *Langobardisaurus*, and *Tanystropheus meridensis* (for critical comments on the use of reduced strict consensus trees see Kearney & Clark, 2003).

The data set obtained from the combination of Benton & Allen's (1997) and Jalil's (1997) data was subsequently combined with the data set offered by Dilkes (1998; 239 characters coded for *Petrolacosaurus* and *Youngina* [outgroup], and *Rhynchosaurus*, *Trilophosaurus*, *Drepanosaurus*, *Megalancosaurus*, *Protorosaurus*, *Prolacerta*, *Macrocnemus*, *Langobardisaurus*, *Tanystropheus longobardicus* [in-group]). Some few characters as defined by Dilkes (1998) are partially overlapping with character definitions offered by Benton & Allen (1997) or Jalil (1997). However, because the character definitions are only partially overlapping, we retained all characters of Dilkes (1997), a strategy that resulted in the partial weighting of the relevant characters. *Proterosuchus* and *Euparkeria* was coded by Dilkes (1998) only. These taxa were accordingly coded for the characters of Benton & Allen (1997) and Jalil (1997) based on published descriptions. Similarly, *Boreopricea* and *Jesairosaurus* had to be coded on the basis of their published descriptions for Dilkes' (1998) characters. Some characters of *Tanystropheus* were coded on the basis of personal observation.

The analysis of this all-inclusive data set with *Euparkeria*, *Proterosuchus*, *Boreopricea*, and *Jesairosaurus* excluded, yielded three equally parsimonious trees (TL = 256; CI = 0.613; RI = 0.625) with a slightly different pattern of protorosaur relationships.

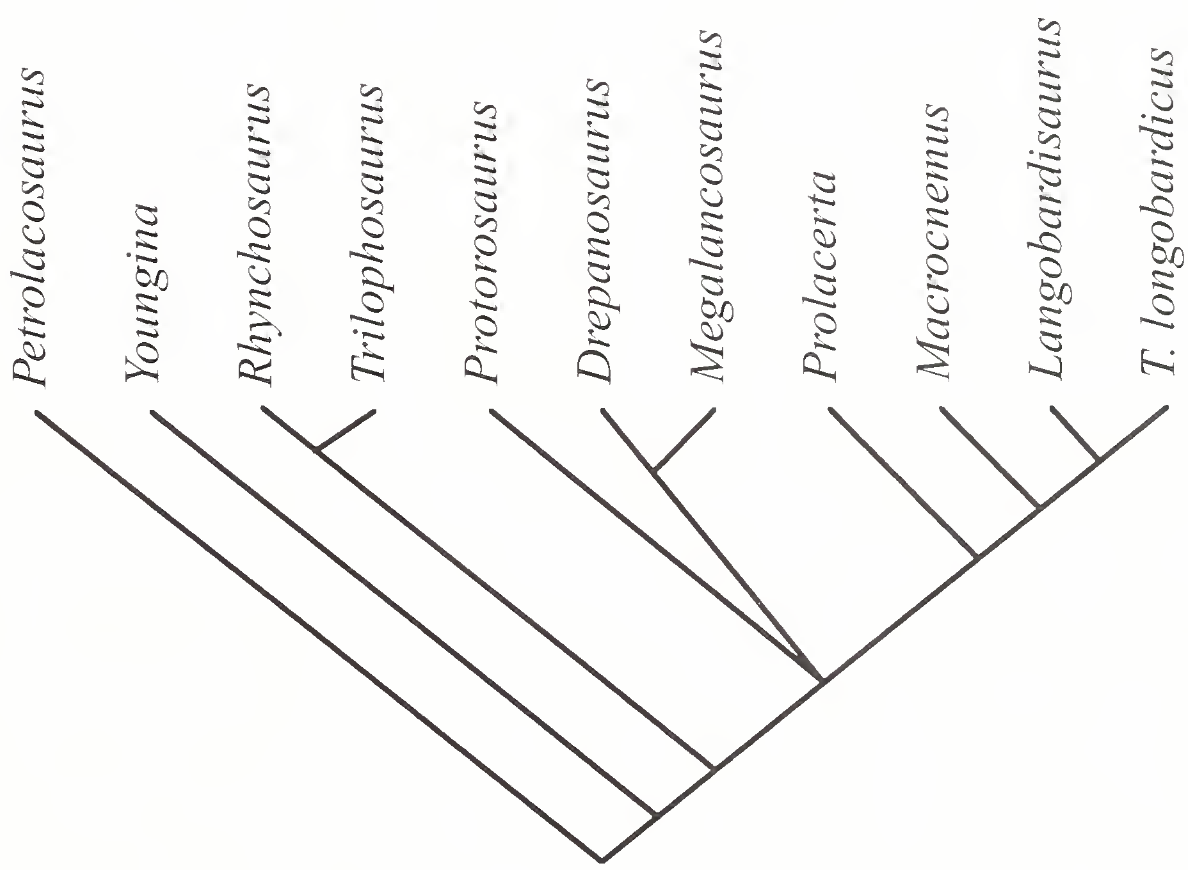

Fig. 2 – The strict consensus tree of the three equally parsimonious cladograms obtained from a combination of the data sets of Benton & Allen (1997), Jalil (1997), and Dilkes (1998). *Euparkeria*, *Proterosuchus*, *Boreopricea* and *Jesairosaurus* excluded.

Fig. 2 – *Strict consensus tree* risultante dai tre cladogrammi con il minor numero di *steps* ottenuti applicando il metodo della parsimonia al set di dati risultante dalla combinazione di quelli di Benton & Allen (1997), Jalil (1997) e Dilkes (1998). *Euparkeria*, *Proterosuchus*, *Boreopricea* e *Jesairosaurus* non sono stati inclusi nell'analisi.

Comparing the two analyses (Figs. 1 and 2) shows the labile position of *Langobardisaurus* that was also identified by RadCon (see comments above). More importantly, the addition of the data offered by Dilkes (1998) shows the traditional Protorosauria to be monophyletic, but again possibly including the *Drepanosaurus* – *Megalancosaurus* clade (which falls into an unresolved trichotomy with *Protorosaurus* and the remaining protorosaurs).

On the other hand, Dilkes (1998) found the protorosaurs paraphyletic, and his result is actually corroborated (Fig. 3) if *Euparkeria* and *Proterosuchus* are added to the data matrix that includes the data from Benton & Allen (1997), Jalil (1997), and Dilkes (1998). The analysis of the all-encompassing data set, now including *Euparkeria* and *Proterosuchus*, resulted in a single most parsimonious tree (TL = 332; CI = 0.542; RI = 0.590) which confirms the paraphyly of the protorosaurs as ordinarily perceived. Other than in Dilkes (1998), however, *Protorosaurus* joins *Prolacerta* and the *Euparkeria* – proterosuchian clade.

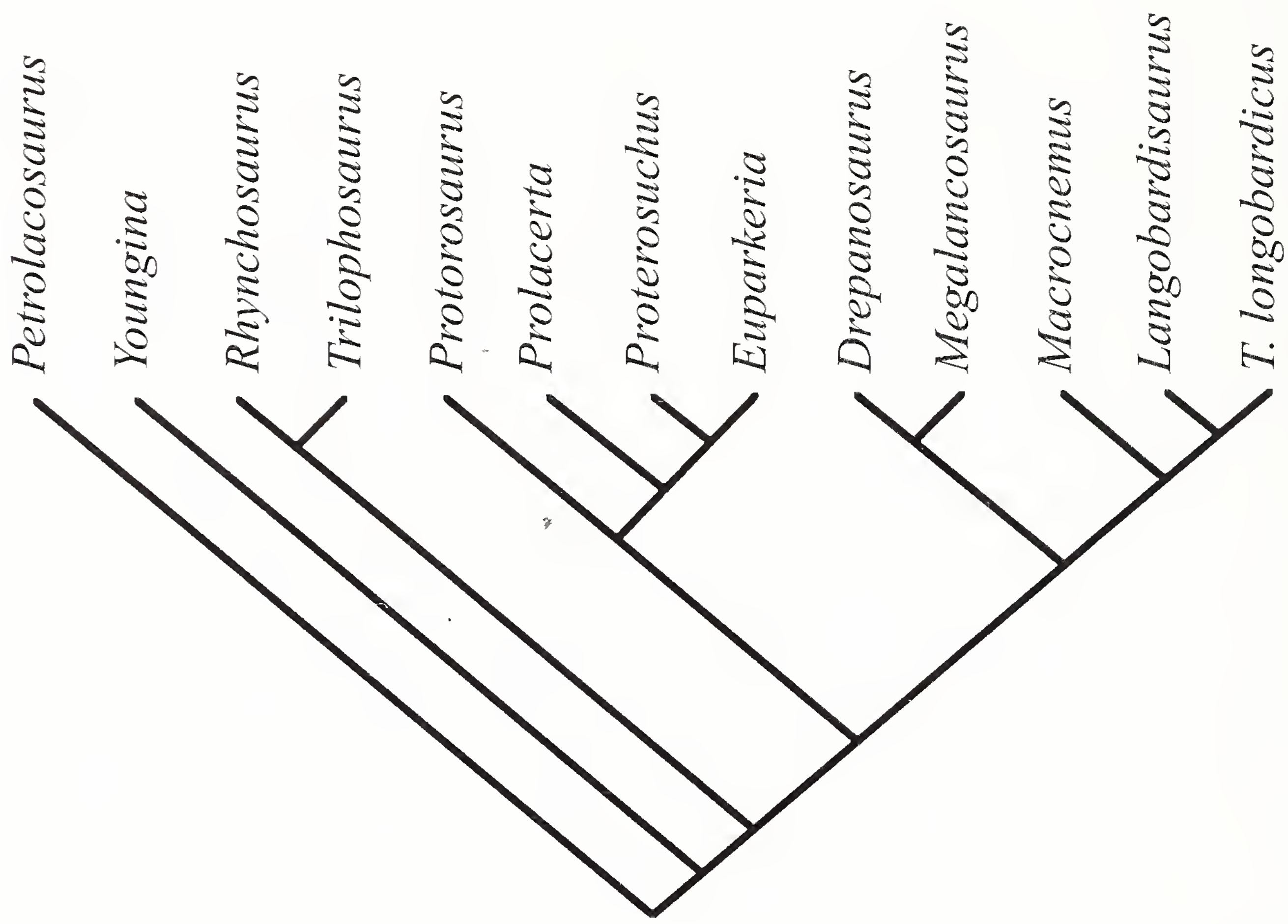

Fig. 3 – Protorosaur paraphyly as obtained from a combination of the data sets of Benton & Allen (1997), Jalil (1997), and Dilkes (1998), after inclusion of *Euparkeria* and *Proterosuchus*.
Fig. 3 – Parafilia dei protorosauri risultante dall'elaborazione dei dati di Benton & Allen (1997), Jalil (1997) e Dilkes (1998) a seguito dell'inclusione dei generi *Euparkeria* e *Proterosuchus*.

The monophyly of the (*Protorosaurus* (*Prolacerta* (*Proterosuchus*, *Euparkeria*))) clade is interesting and supported by several characters (Bremer support index: 1; Bremer, 1988), drawing on all three data sets combined in the analysis (*unequivocal synapomorphies, DELTRAN optimization): BA17 (1); BA41 (1); J34 (1), J62 (1); J63 (1); D59* (1); D88 (2); D91 (2). Even more characters support the (*Prolacerta* (*Proterosuchus*, *Euparkeria*)) clade (Bremer support index: 2): BA14 (1); D15 (1); D17* (1); D26 (0); D42* (1); D46 (1); D48 (1); D51 (1); D53* (1); D58 (1); D75* (1); D87 (2); D89 (1); D113 (1); D116 (1); D117 (1); D122 (1); D126* (1); D142* (1); D143 (1).

Langobardisaurus groups with *Tanystropheus* instead of with *Macrocnemus*,

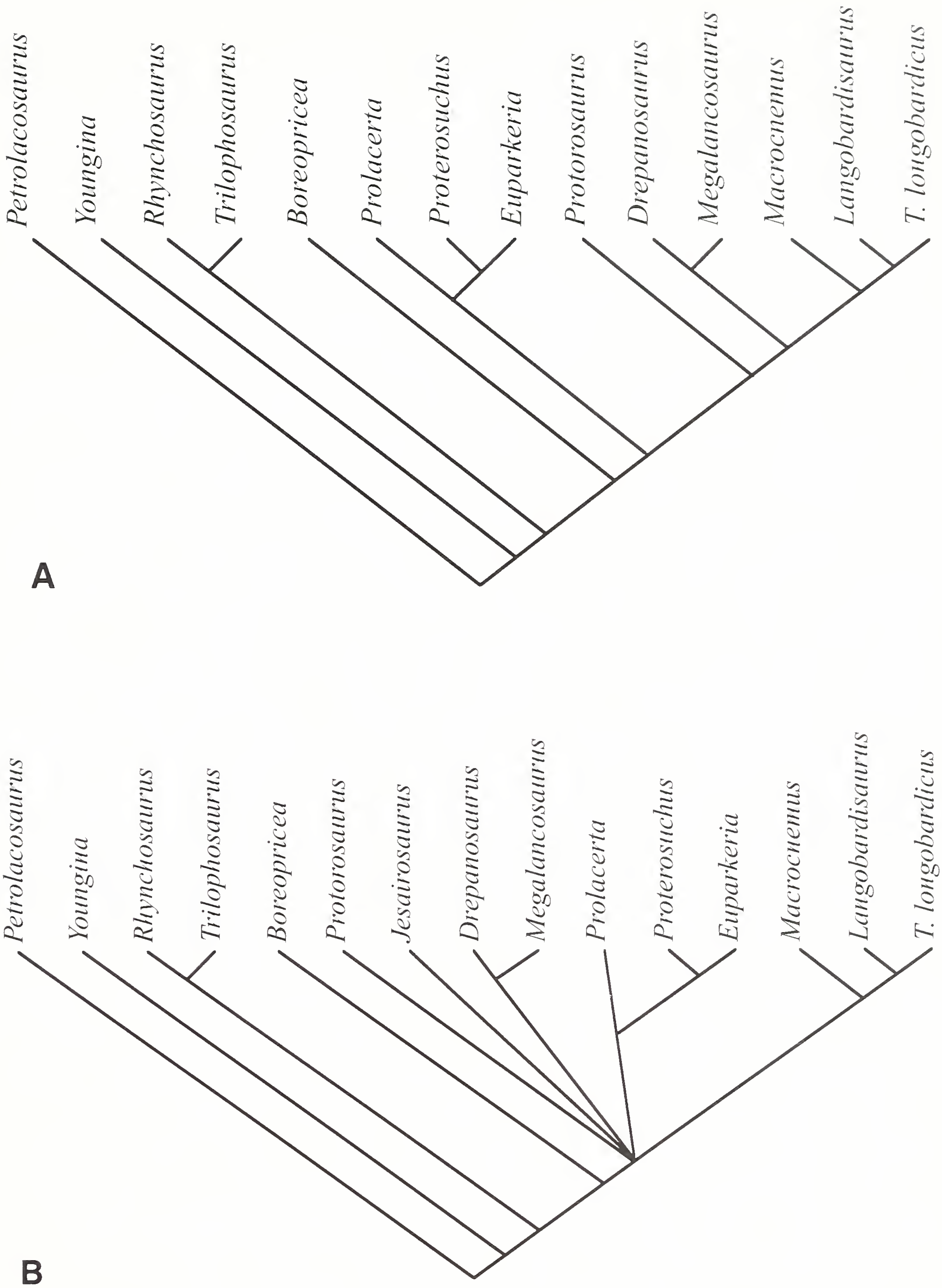

Fig. 4 – Successive addition of *Boreopricea* (A) and *Jesairosaurus* (B) to the matrix that includes the data from Benton & Allen (1997), Jalil (1997), and Dilkes (1998). See text for further discussion.
Fig. 4 – Cladogrammi risultanti dalla successiva inclusione di *Boreopricea* (A) e *Jesairosaurus* (B) nell'elenco dei taxa utilizzati nell'analisi basata sui dati di Benton & Allen (1997), Jalil (1997) e Dilkes (1998). Discussione nel testo.

and those three genera (and presumably their less well known allies) form the sister-clade to a *Drepanosaurus – Megalancosaurus* clade.

In a final analysis, we tested the paraphyly of the Protorosauria as conventionally conceived by successively adding *Boreopricea* and *Jesairosaurus* to the matrix that includes the data from Benton & Allen (1997), Jalil (1997), and Dilkes (1998). The addition of *Boreopricea* results in a single most parsimonious tree (TL = 352; CI = 0.526; RI = 0.576) shown in Fig. 4A. *Prolacerta* remains with proterosuchians, whereas *Protorosaurus* becomes the sister-taxon of a protorosaur clade that includes *Drepanosaurus* and *Megalancosaurus*. Adding *Jesairosaurus* to the analysis breaks the clade that includes *Rhynchosaurus* and *Trilophosaurus*, but otherwise retains the topology of the tree shown in Fig. 3, with *Jesairosaurus* as sister-taxon of a protorosaur clade that includes *Drepanosaurus* and *Megalancosaurus*. Adding both *Boreopricea* and *Jesairosaurus* results in three equally parsimonious trees (TL = 375; CI = 0.515; RI = 0.558) which retain *Prolacerta* as sister-taxon of the *Proterosuchus – Euparkeria* clade. This clade, however, nests in an unresolved polytomy together with *Protorosaurus*, *Jesairosaurus*, and the *Drepanosaurus* and *Megalancosaurus* clade, with a position of *Boreopricea* outside the proterosuchian – protorosaurian assemblage (Fig. 4B). *Macrocnemus* is again recovered as sister-taxon of the *Langobardisaurus – Tanystropheus* clade.

Discussion

Lack of resolution due to missing data caused by incompletely known fossils is a recurrent scheme in the analysis of protorosaurian interrelationships, which ultimately calls for the deletion of very poorly known taxa. The two data sets – one combining the data from Benton & Allen (1997) and Jalil (1997) [referred to here after as the BAJ-data], the other adding those of Dilkes (1998) to the two previous sets [referred to here after as the BAJD-data] – show some striking similarities and differences. Deleting the poorly known taxa *Kadimakara*, *Malerisaurus langstoni* and *Trachelosaurus* from the BAJ-data set results in a well-resolved tree (Fig. 1), which suggests some interesting conclusions: the grouping together of *Drepanosaurus*, *Megalancosaurus* and *Jesairosaurus* in an unresolved trichotomy, as well as the unstable position of *Langobardisaurus* (also indicated by RadCon) relative to *Macrocnemus* and the tanystropheid clade respectively. The sister-group relationship of *Langobardisaurus* with the *Tanystropheus – Tanytrachelos* clade is supported by the BAJD-data set, however.

Cosesaurus was not included in Dilkes' (1998) analysis, but it was included in Peters' (2000) re-analysis of Evans (1988) and Jalil (1997), and while there is no complete resolution amongst the terminals, *Cosesaurus* was found to be relatively more closely related to tanystropheids than to *Macrocnemus* in both these re-analyses (Peters, 2000). The same conclusion is supported by the BAJ-data.

On the basis of the BAJ-data set, both *Boreopricea* and the *Drepanosaurus – Megalancosaurus* clade (with *Jesairosaurus* close to it) nest inside the protorosaurs. On the basis of the BAJD-data set, *Boreopricea* nests outside the (paraphyletic) protorosaur – prolacertiform assemblage at a very basal position amongst archosauromorphs (Fig. 4B), suggesting that *Boreopricea* is a basal archosauromorph rather than a close relative of taxa commonly referred to protorosaurs. This is surprising in view of the fact that Evans (1988) found *Boreopricea* to share a suite of 13 characters with *Cosesaurus*, *Macrocnemus*, and the tanystropheids, a relationship that was recovered by Peters' re-analysis of Evans (1988). By contrast, Peters' (2000) re-analysis of Jalil's (1997) data shows *Boreopricea* in a large basal archosauromorph polytomy outside the *Cosesaurus – Macrocnemus* – tanystropheid assemblage, and the BAJD-data set can be claimed to provide some resolution for the basal archosauromorph polytomy obtained by Peters (2000). Eleven characters exclude *Boreopricea* from the protorosaur – prolacertiform assemblage on the BAJD-data set (DELTRAN; unambiguous synapomorphies*; Bremer support index: 1; *Jesairosaurus* not included): BA2 [1], BA22* [1], J37 [1], J63 [1], J70 [1], D2* [1], D11 [1], D18* [1], D68 [2], D88 [2], D97* [1]. It appears that on the basis of current knowledge, *Boreopricea* could be a basal archosauromorph rather than a member of the protorosaurs, or prolacertiforms.

The BAJ-data set shows *Drepanosaurus* and *Megalancosaurus* in a trichotomy with *Jesairosaurus*, whereas the BAJD-data set invariably shows *Drepanosaurus* and *Megalancosaurus* to be sister-taxa. This is a strong signal (Bremer support index: 11; *Jesairosaurus* not included), supported by 19 characters (DELTRAN; BA28 [1], BA32 [1], BA33 [1], BA38 [1], BA46 [1], J19 [1], J34 [0], D88 [3], D92 [0], D99 [2], D102* [3], D103 [1], D116 [1], D122 [0], D124 [2], D129 [1], D139* [1], D140* [1], D141* [1]), such that the sister-group relationship of these two enigmatic fossils can be considered well established.

The BAJD-data set places the *Drepanosaurus – Megalancosaurus* clade in an unresolved trichotomy with *Protorosaurus* and the remaining protorosaurs as ordinarily conceived (Fig. 2), but it does so only if *Euparkeria* and *Proterosuchus* are not included. Inclusion of these latter two taxa renders the protorosaurs as ordinarily conceived paraphyletic, and the *Drepanosaurus – Megalancosaurus* clade becomes the sister-group of the *Macrocnemus – Langobardisaurus* – tanystropheid clade (Figs. 3, 4A; *Boreopricea* included, *Jesairosaurus* excluded, Bremer support index: 1). The characters that place the *Drepanosaurus – Megalancosaurus* clade as sister-group of the *Macrocnemus – Langobardisaurus* – tanystropheid clade are (DELTRAN; *Boreopricea* included, *Jesairosaurus* excluded): BA24 [1], BA27 [1], BA36* [1], D80* [1], D100* [1], D134 [1].

If *Jesairosaurus* is excluded but *Boreopricea* is included in the analysis of the BAJD-data set, *Protorosaurus* groups as the sister-taxon of a clade that comprises *Drepanosaurus*, *Megalancosaurus*, and the *Macrocnemus – Langobardisaurus* – tanystropheid clade, whereas *Prolacerta* groups with *Euparkeria* and *Proterosuchus*. This in essence replicates Dilkes' (1998) result. If *Jesairosaurus* is included in the analysis of the BAJD-data set, a drop of resolution results in a polytomy within which the (*Prolacerta* (*Euparkeria*, *Proterosuchus*)) clade is retained (Fig. 4B), however. The (*Protorosaurus* (*Prolacerta* (*Euparkeria*, *Proterosuchus*))) clade is only obtained if both *Boreopricea* and *Jesairosaurus* are excluded from the analysis of the BAJD-data set (see above).

Character description and scoring

In addition to problems arising from including incompletely known taxa in the analysis, there are problems associated with the interpretations of the material and the descriptions and diagnoses of the characters themselves.

In any large list of characters that have been compiled from a number of different sources, there are inevitably questions over the accuracy of certain character descriptions and how easy they are to score. For example character 99 of Dilkes (1998) describes the shape of the scapular blade with three character states: tall and rectangular (0), low with a deep caudal concavity (1), or tall and very narrow (2). Clearly "tall" and "narrow" are very subjective terms, and in the case of *Malerisaurus* could conceivably be scored either as (0) or (2). In any event the shape of the scapula in *Megalancosaurus* and *Drepanosaurus* is very different from that of *Langobardisaurus*, yet they are all giving the score of character state (2). There can even be variability in character states from one specimen to another. Thus, for example, the presence or absence of a perforating foramen between the astragalus and calcaneum (Dilkes' character 115) is variably present in both *Macrocnemus* and *Tanystropheus*.

The presence of a hooked fifth metatarsal is another character that has caused confusion. Understanding of what is meant by the term "hooked fifth metatarsal" has been problematic in the past. In lepidosaurians the fifth metatarsal is bent in two planes, but Robinson (1975) makes it clear that the "hooking" refers to the fact that the proximal end of the bone bends medially to contact distal tarsal four. Robinson also noted bending in the plantar-dorsal plane and this she referred to as inflection. When it comes to interpreting Dilkes' character delineations, it becomes a little ambiguous. Dilkes (1998) describes three states for this character: straight (0), hooked without deflection (1), and hooked with deflection (2). He scores *Tanystropheus* and *Langobardisaurus* as (1), yet in *Langobardisaurus* the bone is quite straight, and there is only the merest hint of an angle in many of the *Tanystropheus* specimens that we examined. On the other hand Dilkes (1998) scores this character (0) for *Protorosaurus*, yet Peyer (fig. 46) shows it to be hooked. It seems that this character still causes confusion. Robinson (1975) states that the presence of processes and tubercles on the fifth metatarsal have apparently only been described in hooked metatarsals, and we suggest that it is the presence or absence of a lateral plantar tubercle that is the critical feature.

When dealing with *Boreopricea* we have to be aware that the identities of the tarsals may be suspect. All the bones were glued on a card and apparently came loose at various times (Benton & Allen, 1997). Consequently some bones are now missing, and it is also readily apparent that some were glued back on the card incorrectly. Thus some pedal elements are in plantar view while others are in dorsal view. This could have a significant effect on assigning character states, which in turn could be the underlying cause of the extreme positions of *Boreopricea* in the analysis of Evans (1988) and of Benton & Allen (1997) compared with that of Peters' (2000) re-analysis of Jalil's (1997) data. It may be that this problem can never be satisfactorily resolved.

These are just some examples of the potential problems we currently face when analyzing protorosaurian phylogeny. An important next step must be a detailed reassessment of each of the characters used to date.

Conclusions

The sister-group relationship of *Drepanosaurus* and *Megalancosaurus* may be considered well established, and the clade represents the sister-group of a clade that comprises *Macrocnemus*, *Langobardisaurus*, and tanystropheids. Peters (2000) found *Cosesaurus* and basal pterosaurs to also nest within that clade, an heterodox hypothesis as far as pterosaurs are concerned that merits further investigation. *Boreopricea* is likely to be a basal archosauromorph rather than a protorosaur.

Protorosaur monophyly as traditionally conceived (Evans, 1988; Benton & Allen, 1997; Jalil, 1997) can no longer be maintained (Dilkes, 1998). Although *Prolacerta* was found to be the sister-taxon of a clade that comprises *Euparkeria* and *Proterosuchus* in some analyses, the relationships of *Protorosaurus* was found to be more variable. Inclusion of all reasonably known protorosaur taxa in the analysis of the BAJD-data set shows both *Prolacerta* and *Protorosaurus* in an unresolved relationship relative to the *Euparkeria – Proterosuchus* clade on the one hand, and to the other protorosaurs on the other. This result highlights the need for an intensified study of both, *Prolacerta* and *Protorosaurus*. One problem that is likely to continue to plague the analysis of protorosaur relationships in the future is the lack of resolution caused by the inclusion of very incompletely known taxa in the analysis.

Tab. 1 – Matrix including the data from Benton & Allen (1997) and Jalil (1997). B1-B48: Benton & Allen's characters; J1-J71: Jalil's characters. See text for discussion.
Tab. 1 – Matrice ricavata dalla combinazione dei dati di Benton & Allen (1997) e di Jalil (1997). B1-B48: caratteri di Benton & Allen; J1-J71: caratteri di Jalil. Discussione nel testo.

BAJ	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
3	Rhynchosaurus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
4	Trilophosaurus	0	0	0	1	?	?	0	0	0	0	?	?	?	0	0
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
7	Protorosaurus	?	1	0	0	?	0	?	0	?	?	?	?	?	?	?
8	Boreopricea	?	0	1	?	0	0	0	0	0	1	1	0	0	1	?
9	Kadimakara	?	?	0	0	0	0	0	0	1	0	1	0	0	1	?
10	M. langstoni	?	?	?	0	?	?	?	?	?	0	?	?	?	?	?
11	M. robinsonae	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0
12	Prolacerta	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0
13	Trachelosaurus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
14	Macrocnemus	0	?	0	0	1	0	0	0	0	1	1	0	0	0	1
15	Cosesaurus	?	?	?	?	?	?	?	?	1	0	1	0	?	0	1
16	Langobardisaurus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0
17	T. longobardicus	1	1	1	0	1	1	1	0	1	0	1	1	0	0	0
18	T. meridensis	0	0	0	0	0	0	1	0	1	0	?	1	0	?	0
19	Tanytrachelos	0	1	0	1	0	1	1	1	1	0	?	?	?	0	0
20	Jesairosaurus	?	?	0	?	?	?	0	0	0	?	?	?	?	?	?

BAJ	2	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		B16	B17	B18	B19	B20	B21	B22	B23	B24	B25	B26	B27	B28	B29	B30
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
4	Trilophosaurus	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0
5	Drepanosaurus	?	?	?	?	?	?	?	1	1	?	0	?	1	?	?
6	Megalancosaurus	?	0	0	1	1	0	?	1	?	1	0	1	1	0	0
7	Protorosaurus	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0
8	Boreopricea	?	1	0	1	1	?	?	1	?	0	0	0	0	?	?
9	Kadimakara	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	M. langstoni	?	1	0	1	1	?	?	1	1	0	0	0	0	?	?
11	M. robinsonae	0	1	0	1	1	1	?	1	1	0	0	0	0	?	?
12	Prolacerta	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0
13	Trachelosaurus	?	1	1	1	1	1	1	1	1	0	?	?	?	?	?
14	Macrocnemus	0	1	0	1	1	1	1	1	1	0	1	1	0	0	0
15	Cosesaurus	?	1	0	1	1	?	1	1	1	0	1	?	0	?	?
16	Langobardisaurus	?	1	0	1	1	0	1	0	?	1	1	1	0	0	?
17	T. longobardicus	0	1	1	1	1	1	1	1	?	1	1	0	0	1	1
18	T. meridensis	0	?	?	1	1	?	1	?	?	?	?	?	?	?	?
19	Tanytrachelos	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?
20	Jesairosaurus	?	1	?	?	1	?	?	0	1	1	0	0	?	?	?

Tab. 1 – Continued.
Tab. 1 – Continua.

BAJ	3	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
		B31	B32	B33	B34	B35	B36	B37	B38	B39	B40	B41	B42	B43	B44	B45
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0
4	Trilophosaurus	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
5	Drepanosaurus	?	1	1	1	0	1	1	1	0	0	1	0	0	0	0
6	Megalancosaurus	?	1	1	0	1	?	0	1	0	0	1	0	0	0	0
7	Protorosaurus	0	?	1	1	?	0	0	0	0	0	1	0	0	0	1
8	Boreopricea	?	1	0	?	?	?	?	0	0	1	1	0	?	?	0
9	Kadimakara	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	M. langstoni	?	?	?	0	1	0	0	0	0	?	?	?	?	?	?
11	M. robinsonae	?	?	?	0	1	0	0	0	0	1	1	1	1	1	0
12	Prolacerta	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
13	Trachelosaurus	?	?	?	?	1	?	?	0	?	?	?	?	?	?	?
14	Macrocnemus	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1
15	Cosesaurus	?	1	0	0	?	?	0	0	0	1	0	0	1	1	1
16	Langobardisaurus	?	0	0	?	?	1	1	0	0	1	0	0	?	?	1
17	T. longobardicus	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1
18	T. meridensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Tanytrachelos	?	1	1	1	1	?	1	0	1	0	?	1	1	1	1
20	Jesairosaurus	?	?	?	?	1	?	0	1	?	?	?	?	?	?	?

BAJ	4	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
		B46	B47	B48	J1	J2	J3	J4	J5	J6	J7	J8	J9	J10	J11	J13
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	0	0	0	1	1	1	1	1	?	1	1	1	?	1	1
4	Trilophosaurus	0	0	0	?	1	1	1	1	1	1	1	1	?	1	1
5	Drepanosaurus	1	?	0	?	?	?	?	?	?	?	?	1	?	0	?
6	Megalancosaurus	1	1	?	?	?	?	?	?	?	?	?	1	0	1	?
7	Protorosaurus	0	?	0	1	1	1	1	1	?	?	1	1	?	1	1
8	Boreopricea	0	1	?	?	?	?	1	1	?	?	?	1	?	1	1
9	Kadimakara	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1
10	M. langstoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
11	M. robinsonae	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	Prolacerta	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
13	Trachelosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Macrocnemus	0	?	0	?	1	1	1	1	?	?	1	1	?	1	1
15	Cosesaurus	1	1	?	?	?	?	1	?	?	?	1	1	?	1	?
16	Langobardisaurus	0	0	?	?	?	?	?	?	?	?	?	?	?	1	?
17	T. longobardicus	1	1	1	1	1	?	1	1	?	1	1	1	1	1	1
18	T. meridensis	?	?	?	1	1	?	1	1	?	1	1	1	?	?	1
19	Tanytrachelos	1	1	1	?	?	?	1	?	?	?	1	1	?	1	1
20	Jesairosaurus	?	?	?	?	1	1	1	1	?	1	1	1	?	?	1

BAJ	5	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
		J14	J15	J16	J17	J18	J19	J20	J21	J23	J24	J25	J26	J28	J29	J30
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	?	?	1	0	?	0	0	0	0	0	0	0
3	Rhynchosaurus	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1
4	Trilophosaurus	1	?	0	?	0	0	0	0	0	0	1	0	0	1	1
5	Drepanosaurus	?	?	?	?	?	1	?	?	1	0	?	?	?	1	?
6	Megalancosaurus	?	?	?	?	?	1	?	0	0	0	?	1	?	?	?
7	Protorosaurus	1	1	1	0	0	0	0	?	0	0	?	?	1	1	1
8	Boreopricea	?	1	1	0	0	?	0	0	0	0	1	1	0	1	1
9	Kadimakara	?	1	?	0	?	?	?	?	?	?	?	?	0	?	?
10	M. langstoni	?	?	?	0	?	?	0	0	?	?	?	?	0	1	1
11	M. robinsonae	?	?	?	0	?	?	0	0	?	?	?	?	?	1	1
12	Prolacerta	1	?	0	0	0	0	0	0	0	0	1	1	0	1	1
13	Trachelosaurus	?	?	?	?	?	?	0	?	?	?	?	?	?	1	?
14	Macrocnemus	1	1	?	0	?	0	0	0	0	0	1	1	0	1	1
15	Cosesaurus	?	?	?	?	?	?	?	0	?	?	1	?	?	?	?
16	Langobardisaurus	?	?	?	?	?	0	0	0	0	?	1	?	1	1	1
17	T. longobardicus	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1
18	T. meridensis	1	1	0	0	0	?	?	?	?	?	1	1	0	1	1
19	Tanytrachelos	?	?	?	?	?	0	?	?	0	0	?	?	0	1	1
20	Jesairosaurus	1	?	?	0	?	?	0	1	?	?	1	?	0	0	?

Tab. 1 – Continued.
Tab. 1 – Continua.

BAJ	6	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
		J31	J34	J36	J37	J38	J42	J45	J47	J48	J49	J52	J62	J63	J64	J65
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?
3	Rhynchosaurus	1	1	0	0	0	0	0	?	0	0	0	0	0	0	0
4	Trilophosaurus	1	1	1	1	0	0	0	0	0	?	0	0	0	0	0
5	Drepanosaurus	1	0	?	?	?	?	?	?	0	?	0	?	?	?	?
6	Megalancosaurus	1	0	?	?	1	?	0	0	0	?	0	?	?	1	?
7	Protorosaurus	1	1	1	1	1	0	0	0	0	?	0	1	1	1	?
8	Boreopricea	?	?	?	?	1	0	?	0	?	0	1	1	0	1	?
9	Kadimakara	?	?	?	?	?	1	?	?	?	?	?	?	1	?	?
10	M. langstoni	1	?	?	?	?	?	0	?	0	?	?	?	?	1	?
11	M. robinsonae	1	?	?	?	?	?	0	?	0	?	?	?	?	1	?
12	Prolacerta	1	1	1	1	1	1	0	?	0	0	0	1	1	1	1
13	Trachelosaurus	1	?	1	1	?	?	?	?	0	?	?	?	?	?	?
14	Macrocnemus	1	0	1	1	1	1	1	0	1	1	0	1	1	1	?
15	Cosesaurus	?	?	1	1	1	?	1	1	1	?	1	1	?	1	?
16	Langobardisaurus	1	1	1	1	?	?	1	?	?	?	0	?	0	1	?
17	T. longobardicus	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0
18	T. meridensis	?	?	1	1	1	1	?	?	?	?	?	0	0	1	0
19	Tanytrachelos	1	1	1	1	?	?	1	?	?	?	1	1	?	1	?
20	Jesairosaurus	1	?	1	?	1	1	0	?	0	?	?	?	1	1	?

BAJ	7	91	92	93	94	95
		J66	J68	J69	J70	J71
1	Petrolacosaurus	0	0	?	?	0
2	Youngina	0	0	0	0	?
3	Rhynchosaurus	1	1	0	0	0
4	Trilophosaurus	0	1	1	1	0
5	Drepanosaurus	?	?	?	?	0
6	Megalancosaurus	?	?	?	?	0
7	Protorosaurus	1	?	?	?	0
8	Boreopricea	1	?	?	?	0
9	Kadimakara	?	?	?	?	?
10	M. langstoni	1	?	?	?	?
11	M. robinsonae	1	?	?	?	?
12	Prolacerta	1	1	1	1	0
13	Trachelosaurus	?	?	?	?	?
14	Macrocnemus	?	?	?	?	0
15	Cosesaurus	?	?	?	?	0
16	Langobardisaurus	?	?	?	?	1
17	T. longobardicus	1	?	?	1	1
18	T. meridensis	1	?	?	?	?
19	Tanytrachelos	?	?	?	?	1
20	Jesairosaurus	1	?	?	?	?

Tab. 2 - Matrix including the data from Benton & Allen (1997), Jalil (1997), and Dilkes (1998). B1-B48: Benton & Allen's characters; J1-J71: Jalil's characters; D1-D144: Dilkes' characters. See text for discussion.
Tab. 2 – Matrice ricavata dalla combinazione dei dati di Benton & Allen (1997), di Jalil (1997) e di Dilkes (1998). B1-B48: caratteri di Benton & Allen; J1-J71: caratteri di Jalil; D1-D144: caratteri di Dilkes. Discussione nel testo.

BAJD	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
3	Rhynchosaurus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
4	Trilophosaurus	0	0	0	1	?	?	0	0	0	0	?	?	?	0	0
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
7	Protorosaurus	?	1	0	0	?	0	?	0	?	?	?	?	?	?	?
8	Prolacerta	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0
9	Macrocnemus	0	?	0	0	1	0	0	0	0	1	1	0	0	0	1
10	Langobardisaurus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0
11	T. longobardicus	1	1	1	0	1	1	1	0	1	0	1	1	0	0	0
12	Proterosuchus	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1
13	Euparkeria	0	1	0	1	0	0	1	0	0	0	0	0	1	1	0
14	Jesairosaurus	?	?	0	?	?	?	0	0	0	?	?	?	?	?	?
15	Boreopricea	?	0	1	?	0	0	0	0	0	1	1	0	0	1	?

BAJD	2	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		B16	B17	B18	B19	B20	B21	B22	B23	B24	B25	B26	B27	B28	B29	B30
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
4	Trilophosaurus	1	0	0	0	? 0	0	0	1	0	0	0	0	1	0	0
5	Drepanosaurus	?	?	?	?	?	?	?	1	1	?	0	?	1	?	?
6	Megalancosaurus	?	0	0	1	1	0	?	1	?	1	0	1	1	0	0
7	Protorosaurus	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0
8	Prolacerta	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0
9	Macrocnemus	0	1	0	1	1	1	1	1	1	0	1	1	0	0	0
10	Langobardisaurus	?	1	0	1	1	0	1	0	?	1	1	1	0	0	?
11	T. longobardicus	0	1	1	1	1	1	1	1	?	1	1	0	0	1	1
12	Proterosuchus	0	1	0	0	0	?	1	1	1	0	0	0	0	0	0
13	Euparkeria	0	0	0	0	0	?	?	1	0	0	0	1	0	?	?
14	Jesairosaurus	?	1	?	?	1	?	?	0	1	1	0	0	?	?	?
15	Boreopricea	?	1	0	1	1	?	?	1	?	0	0	0	0	?	?

BAJD	3	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
		B31	B32	B33	B34	B35	B36	B37	B38	B39	B40	B41	B42	B43	B44	B45
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0
4	Trilophosaurus	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
5	Drepanosaurus	?	1	1	1	0	1	1	1	0	0	1	0	0	0	0
6	Megalancosaurus	?	1	1	0	1	?	0	1	0	0	1	0	0	0	0
7	Protorosaurus	0	?	1	1	?	0	0	0	0	0	1	0	0	0	1
8	Prolacerta	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
9	Macrocnemus	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1
10	Langobardisaurus	?	0	0	?	?	1	1	0	0	1	0	0	?	?	1
11	T. longobardicus	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1
12	Proterosuchus	0	0	0	1	1	0	1	0	0	0	1	1	0	0	1
13	Euparkeria	?	?	?	1	1	0	1	0	0	1	1	1	1	1	0
14	Jesairosaurus	?	?	?	?	1	?	0	1	?	?	?	?	?	?	?
15	Boreopricea	?	1	0	?	?	?	?	0	0	1	1	0	?	?	0

Tab. 2 – Continued.
Tab. 2 – Continua.

BAJD	4	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
		B46	B47	B48	J1	J2	J3	J4	J5	J6	J7	J8	J9	J10	J11	J13
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	0	0	0	1	1	1	1	1	?	1	1	1	?	1	1
4	Trilophosaurus	0	0	0	?	1	1	1	1	1	1	1	1	?	1	1
5	Drepanosaurus	1	?	0	?	?	?	?	?	?	?	?	1	?	0	?
6	Megalancosaurus	1	1	?	?	?	?	?	?	?	?	?	1	0	1	?
7	Protorosaurus	0	?	0	1	1	1	1	1	?	?	1	1	?	1	1
8	Prolacerta	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
9	Macrocnemus	0	?	0	?	1	1	1	1	?	?	1	1	?	1	1
10	Langobardisaurus	0	0	?	?	?	?	?	?	?	?	?	?	?	1	?
11	T. longobardicus	1	1	1	1	1	?	1	0	?	1	1	1	1	1	1
12	Proterosuchus	0	0	0	0	1	1	1	1	?	?	0	1	0	1	0
13	Euparkeria	0	0	0	0	1	1	1	1	?	1	0	1	?	1	0
14	Jesairosaurus	?	?	?	?	1	1	1	1	?	1	1	1	?	?	1
15	Boreopricea	0	1	?	?	?	?	1	1	?	?	?	1	?	1	1

BAJD	5	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
		J14	J15	J16	J17	J18	J19	J20	J21	J23	J24	J25	J26	J28	J29	J30
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	?	?	1	0	?	0	0	0	0	0	0	0
3	Rhynchosaurus	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1
4	Trilophosaurus	1	?	0	?	0	0	0	0	0	0	1	0	0	1	1
5	Drepanosaurus	?	?	?	?	?	1	?	?	1	0	?	?	?	1	?
6	Megalancosaurus	?	?	?	?	?	1	?	0	0	0	?	1	?	?	?
7	Protorosaurus	1	1	1	0	0	0	0	?	0	0	?	?	1	1	1
8	Prolacerta	1	?	0	0	0	0	0	0	0	0	1	1	0	1	1
9	Macrocnemus	1	1	?	0	?	0	0	0	0	0	1	1	0	1	1
10	Langobardisaurus	?	?	?	?	?	0	0	0	0	?	1	?	1	1	1
11	T. longobardicus	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1
12	Proterosuchus	0	0	0	0	?	1	?	0	0	0	1	0	1	1	1
13	Euparkeria	0	0	0	0	?	1	?	0	0	1	1	0	1	1	1
14	Jesairosaurus	1	?	?	0	?	?	0	1	?	?	1	?	0	0	?
15	Boreopricea	?	1	1	0	0	?	0	0	0	0	1	1	0	1	1

BAJD	6	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
		J31	J34	J36	J37	J38	J42	J45	J47	J48	J49	J52	J62	J63	J64	J65
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?
3	Rhynchosaurus	1	1	0	0	0	0	0	?	0	0	0	0	0	0	0
4	Trilophosaurus	1	1	1	1	0	0	0	0	0	?	0	0	0	0	0
5	Drepanosaurus	1	0	?	?	?	?	?	?	0	?	0	?	?	?	?
6	Megalancosaurus	1	0	?	?	1	?	0	0	0	?	0	?	?	1	?
7	Protorosaurus	1	1	1	1	1	0	0	0	0	?	0	1	1	1	?
8	Prolacerta	1	1	1	1	1	1	0	?	0	0	0	1	1	1	1
9	Macrocnemus	1	0	1	1	1	1	1	0	1	1	0	1	1	1	?
10	Langobardisaurus	1	1	1	1	?	?	1	?	?	?	0	?	0	1	?
11	T. longobardicus	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0
12	Proterosuchus	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0
13	Euparkeria	1	1	0	1	1	0	0	?	0	1	1	1	1	1	0
14	Jesairosaurus	1	?	1	?	1	1	0	?	0	?	?	?	1	1	?
15	Boreopricea	?	?	?	?	1	0	?	0	?	0	1	1	0	1	?

Tab. 2 – Continued.
Tab. 2 – Continua.

BAJD	7	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
		J66	J68	J69	J70	J71	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
1	Petrolacosaurus	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	1	1	0	0	0	0	0	0	?	0	1	1	1	1	1
4	Trilophosaurus	0	1	1	1	0	0	0	1	?	0	0	0	1	1	0
5	Drepanosaurus	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	?	?	?	?	0	0	1	?	?	?	0	?	1	0	0
7	Protorosaurus	1	?	?	?	0	0	1	0	1	0	0	?	1	0	0
8	Prolacerta	1	1	1	1	0	0	1	0	1	0	0	0	1	0	0
9	Macrocnemus	?	?	?	?	0	0	1	?	1	0	0	0	1	0	?
10	Langobardisaurus	?	?	?	?	1	?	?	0	?	?	0	?	?	0	?
11	T. longobardicus	1	?	?	1	1	0	1	0	1	0	0	0	1	0	0
12	Proterosuchus	1	?	?	?	0	0	1	0	0	1	1	0	1	0	0
13	Euparkeria	1	?	?	?	0	0	1	0	0	1	0	0	1	0	0
14	Jesairosaurus	1	?	?	?	?	0	1	0	1	0	0	?	?	0	?
15	Boreopricea	1	?	?	?	0	0	?	?	1	?	?	?	?	?	0

BAJD	8	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
		D11	D12	D13	D14	D15	D16	D17	D18	D19	D20	D21	D22	D23	D24	D25
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	?	1	0	0	0	0	0	0	1	0	0	0
3	Rhynchosaurus	1	1	1	1	2	1	0	0	1	?	?	0	1	0	1
4	Trilophosaurus	0	1	0	1	1	0	0	0	0	0	0	0	?	1	0
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	1	1	?	?	?	0	?	?	?	?	?	?	?	?	?
7	Protorosaurus	?	?	?	?	2	0	?	1	0	?	?	?	0	?	1
8	Prolacerta	1	1	0	?	1	0	1	1	0	0	0	0	0	0	0
9	Macrocnemus	1	1	0	?	2	0	0	1	0	0	0	0	0	1	0
10	Langobardisaurus	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?
11	T. longobardicus	1	1	0	?	2	0	0	1	0	0	0	2	0	1	1
12	Proterosuchus	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0
13	Euparkeria	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0
14	Jesairosaurus	?	?	?	?	?	0	0	?	?	0	0	0	0	1	1
15	Boreopricea	0	?	1	?	0	1	0	0	0	0	0	0	0	0	0

BAJD	9	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
		D26	D27	D28	D28	D30	D31	D32	D33	D34	D35	D36	D37	D38	D39	D40
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0
3	Rhynchosaurus	2	1	1	1	1	0	1	1	2	0	1	1	?	0	1
4	Trilophosaurus	2	1	1	1	1	?	1	0	?	?	1	1	0	0	?
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Protorosaurus	2	1	1	?	?	?	0	0	2	?	?	?	?	?	?
8	Prolacerta	0	0 & 1	1	1	1	0	1	0	2	1	1	1	0	?	1
9	Macrocnemus	1	1	1	?	?	?	1	0	2	1	1	1	?	?	?
10	Langobardisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	T. longobardicus	2	0	1	1	1	0	1	0	2	2	1	1	0	0	1
12	Proterosuchus	0	1	1	0	1	0	1	0	2	0	1	1	1	1	1
13	Euparkeria	0	1	1	0	1	1	1	0	2	0	1	1	1	1	0
14	Jesairosaurus	0	?	?	?	?	1	0	0	1	?	1	?	?	?	?
15	Boreopricea	0	?	0	?	?	?	0	0	?	1	1	1	?	?	?

Tab. 2 – Continued.
Tab. 2 – Continua.

BAJD	10	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
		D41	D42	D43	D44	D45	D46	D47	D48	D49	D50	D51	D52	D53	D54	D55
1	Petrolacosaurus	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
2	Youngina	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0
3	Rhynchosaurus	1	2	0	1	1	0	1	1	1	0	1	1	0	1	1
4	Trilophosaurus	0	?	0	1	1	?	1	1	?	0	1	1	0	0	1
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
7	Protorosaurus	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0
8	Prolacerta	0	1	0	1	1	1	1	1	1	0	1	1	1	0	0
9	Macrocnemus	?	?	1	?	?	?	?	?	?	0	?	?	?	?	0
10	Langobardisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
11	T. longobardicus	0	2	1	1	0	?	1	0	?	0	0	1	0	0	0
12	Proterosuchus	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0
13	Euparkeria	0	1	1	1	0	1	1	1	1	1	1	1	1	0	0
14	Jesairosaurus	?	?	?	1	?	?	?	?	?	?	1	?	?	0	0
15	Boreopricea	?	?	?	?	?	?	?	?	?	?	1	1	0	?	0

BAJD	11	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
		D56	D57	D58	D59	D60	D61	D62	D63	D64	D65	D66	D67	D68	D69	D70
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	1	0	0	0	1	1	2	1	2	2	1	1	3	2	0
4	Trilophosaurus	1	0	0	0	0	0	0	0	0	0	1	1	3	2	0
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	Megalancosaurus	1	0	0	0	0	0	0	0	0	0	?	?	?	?	0
7	Protorosaurus	1	0	0	1	0	0	0	0	0	0	0	0	?	?	0
8	Prolacerta	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0
9	Macrocnemus	1	0	1	0	0	0	0	0	0	0	0	0	2	2	0
10	Langobardisaurus	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?
11	T. longobardicus	1	0	0	0	0	0	0	0	0	0	0	1	3	2	0
12	Proterosuchus	1	1	1	1	0	0	0	0	0	0	0	0	2	0	0
13	Euparkeria	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0
14	Jesairosaurus	1	0	0	?	?	0	?	0	0	0	?	0	0	1	0
15	Boreopricea	1	0	1	0	0	0	?	0	0	0	?	0	?	?	0

BAJD	12	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
		D71	D72	D73	D74	D75	D76	D77	D78	D79	D80	D81	D82	D83	D84	D85
1	Petrolacosaurus	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
2	Youngina	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
3	Rhynchosaurus	1	1	1	2	?	0	?	?	?	?	0	0	1	?	0
4	Trilophosaurus	0	0	1	2	0	0	1	1	1	0	0	0	1	1	0
5	Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0
6	Megalancosaurus	?	0	0	?	?	0	?	?	1	1	2	1	1	1	0
7	Protorosaurus	0	0	0	?	?	0	1	1	1	?	2	1	?	?	0
8	Prolacerta	0	0	1	2	1	0	1	1	1	0	2	1	1	1	0
9	Macrocnemus	0	0	1	2	0	0	1	1	1	1	2	1	1	?	1
10	Langobardisaurus	?	0	?	?	?	?	1	1	1	1	2	1	1	?	1
11	T. longobardicus	0	0	1	2	0	0	1	1	1	1	2	1	1	0	1
12	Proterosuchus	0	0	0	2	1	1	1	1	0	0	?	0	1	1	0
13	Euparkeria	0	0	0	2	1	1	1	1	0	0	0	0	1	1	0
14	Jesairosaurus	0	?	0	2	0	0	1	1	?	1	?	0	1	?	0
15	Boreopricea	0	0	?	?	?	0	?	?	?	?	0	0	1	?	0

Tab. 2 – Continued.
Tab. 2 – Continua.

BAJD	13	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
		D86	D87	D88	D89	D90	D91	D92	D93	D94	D95	D96	D97	D98	D99	D100
1	Petrolacosaurus	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
2	Youngina	1	0	0	0	1	0	0	?	0	1	0	0	0	0	?
3	Rhynchosaurus	1	0	3	0	1	0	1	1	0	?	1	0	1	0	0
4	Trilophosaurus	1	0	1	?	1	0	1	1	0	1	0	?	1	0	0
5	Drepanosaurus	1	0	3	0	1	0	0	1	?	?	?	?	?	2	1
6	Megalancosaurus	1	0	3	?	?	2	0	1	0	?	?	?	?	2	?
7	Protorosaurus	1	0	2	?	?	2	1	?	?	?	?	?	?	0	0
8	Prolacerta	1	2	2	1	1	2	1	1	0	1	0	1	0	0	0
9	Macrocnemus	1	1	0	1	1	1	1	1	0	1	0	1	0	1	1
10	Langobardisaurus	?	1	0	1	1	?	1	1	0	1	?	?	?	2	1
11	T. longobardicus	1	0	0	1	1	0	1	1	0	0	0	?	0	1	1
12	Proterosuchus	1	1	2	1	1	2	1	1	0	1	1	1	0	0	0
13	Euparkeria	1	2	2	1	1	1	1	1	0	1	1	?	0	0	0
14	Jesairosaurus	?	0	0	?	0	?	1	1	?	0	1	?	0	0	0
15	Boreopricea	?	?	1	0	?	?	?	?	?	?	?	?	?	0	?

BAJD	14	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
		D101	D102	D103	D104	D105	D106	D107	D108	D109	D110	D111	D112	D113	D114	D115
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	1	1	0	0	0	1	0	0	0	1	0	0	0	?	0
3	Rhynchosaurus	1	1	0	0	0	1	1	0	?	?	0	1	1	0	1
4	Trilophosaurus	1	1	1	0	0	1	1	0	1	1	0	0	1	0	0
5	Drepanosaurus	1	3	1	0	?	1	1	0	?	1	0	0	?	1	0
6	Megalancosaurus	1	3	1	0	?	1	1	0	?	1	0	0	0	0	0
7	Protorosaurus	1	?	?	?	?0	1	1	0	?	1	0	0	?	0	0
8	Prolacerta	1	1	0	1	0	1	1	0	1	1	0	0	1	0	0
9	Macrocnemus	1	1	0	0	1	1	1	0	?	1	0	0	0	0	0
10	Langobardisaurus	1	?	1	0	?	1	1	0	?	1	0	0	1	0	0
11	T. longobardicus	1	1	0	0	1	1	1	0	1	0	0	0	0	0	?
12	Proterosuchus	1	1	0	0	0	1	1	0	?	1	0	0	1	0	0
13	Euparkeria	1	1	1	1	0	1	1	0	?	1	0	0	1	0	1
14	Jesairosaurus	?	2	?	?	?	0	1	1	?	?	?	?	?	?	?
15	Boreopricea	?	?	?	?	?	1	1	1	?	1	0	0	?	0	?

BAJD	15	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225
		D116	D117	D118	D119	D120	D121	D122	D123	D124	D125	D126	D127	D128	D129	D130
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0
3	Rhynchosaurus	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0
4	Trilophosaurus	1	1	0	0	0	1	1	0	0	0	?	0	0	0	0
5	Drepanosaurus	1	0	0	0	0	0	0	0	2	?	?	?	0	1	?
6	Megalancosaurus	1	0	0	0	0	1	0	0	2	?	?	0	?	1	?
7	Protorosaurus	0	0	0	0	0	1	0	0	0	?	?	0	0	0	?
8	Prolacerta	1	1	0	0	0	?	1	0	1	0	1	0	0	0	0
9	Macrocnemus	0	1	0	0	1	1	1	0	1	0	?	0	0	0	0
10	Langobardisaurus	0	1	0	1	1	1	1	0	1	?	?	0	0	?	?
11	T. longobardicus	0	?	?	1	1	1	1	0	2	0	0	0	0	0	0
12	Proterosuchus	1	1	0	0	0	1	1	1	?	0	1	0	0	0	0
13	Euparkeria	1	?	?	1	1	1	1	0	?	0	1	0	0	?	0
14	Jesairosaurus	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?
15	Boreopricea	0	?	?	0	?	1	1	?	?	0	?	0	?	0	?

Tab. 2 – Continued.
Tab. 2 – Continua.

BAJD	16	226	227	228	229	230	231	232	233	234	235	236	237	238	239
		D131	D132	D133	D134	D135	D136	D137	D138	D139	D140	D141	D142	D143	D144
1	Petrolacosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Youngina	0	0	?	0	0	0	0	0	0	0	0	0	1	0
3	Rhynchosaurus	0	0	0	0	0	0	0	?	0	0	0	0	0	0
4	Trilophosaurus	0	0	0	0	0	0	1	0	0	0	0	?	0	0
5	Drepanosaurus	0	?	?	?	?	?	0	0	1	1	1	?	?	0
6	Megalancosaurus	0	0	?	1	0	0	0	0	1	1	1	?	0	?
7	Protorosaurus	0	0	?	0	1	0	?	0	0	0	0	?	0	0
8	Prolacerta	0	0	0	1	0	0	0	0	0	0	0	1	1	0
9	Macrocnemus	0	0	?	1	1	0	1	0	0	0	0	?	1	0
10	Langobardisaurus	0	0	?	1	1	1	2	1	0	0	0	?	1	?
11	T. longobardicus	0	0	?	1	1	1	2	1	0	0	0	0	0	0
12	Proterosuchus	0	0	?	0	0	0	1	0	0	0	0	1	1	0
13	Euparkeria	0	0	0	0	0	0	0	0	0	0	0	1	1	0
14	Jesairosaurus	?	0	?	?	?	0	0	?	?	0	?	?	?	?
15	Boreopricea	?	?	?	0	?	0	?	0	?	?	?	?	0	?

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References

Bartholomai A., 1979 - New lizard-like reptiles from the Early Triassic of Queensland. *Alcheringa*, 3: 225-234.

Benton M.J., 1985 - Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84: 97-164.

Benton M.J. & Allen J.L., 1997 - *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles. *Palaeontology*, 40: 931-953.

Benton M.J. & Walker A.D., 1996 - *Rhombopholis*, a prolacertiform reptile from the Middle Triassic of England. *Palaeontology*, 39: 763-782.

Berman D.S. & Reisz R., 1992 - *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of North-Central New Mexico. *Journal of Paleontology*, 66: 1001-1009.

Bizzarini F. & Muscio G., 1994 - Un nuovo rettile (Reptilia, Prolacertiformes) dal Norico di Preone (Udine, Italia Nordorientale). Nota preliminare. *Gortania – Atti Museo Friulano Storia Naturale*, 16: 67-76.

Bremer K., 1988 - The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, 42: 795-803.

Broili F. & Fischer E., 1917 - *Trachelosaurus fischeri* nov. gen. nov. sp. Ein neuer Saurier aus dem Buntsandstein von Bernburg. *Jahrbuch der Königlichen Preussischen Geologischen Landesanstalt*, 37: 359-414.

Calzavara M., Muscio G. & Wild R., 1981 - *Megalancosaurus preonensis* n.g., n. sp., a new reptile from the Norian of Friuli, Italy. *Gortania – Atti Museo Friulano Storia Naturale*, 2: 49-64.

Chatterjee S., 1980 - *Malerisaurus*, a new eosuchian reptile from the Late Triassic of India. *Philosphical Transactions of the Royal Society of London*, 291: 163-200.

Chatterjee S., 1986 - *Malerisaurus langstoni*, a new diapsid reptile from the Triassic of Texas. *Journal of Vertebrate Paleontology*, 6: 297-312.

Colbert E.H. & Olsen P.E., 2001 - A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). *American Museum Novitates*, 3334: 1-24.

Dilkes D.W., 1998 - The early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Transactions of the Royal Society of London*, B 353: 501-541.

Ellenberger P. & Villalta J.F., 1974 - Sur la présence d'un ancêtre probable des Oiseaux dans le Muschelkalk supérieur de Catalogne (Espagne). Note préliminaire. *Acta Geológica Hispánica*, IX (5): 162-168.

Ellenberger P., 1977 - Quelques précisions sur l'anatomie et la place systématique très spéciale de *Cosesaurus aviceps* (Ladinien supérieur de Montral, Catalogne). *Cuadernos de Geología Ibérica*, 4: 169-188.

Ellenberger P., 1978 - L'origine des oiseaux. Historique et méthodes nouvelles. Les problèmes des Archaeornithes. La venue au jour de *Cosesaurus aviceps* (Muschelkalk supérieur). *Mém. Trav. E.P.H.E. Inst. Montpellier*, 4: 91-117.

Evans E.S., 1988 - The early history and relationships of the Diapsida. In: The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds. Benton M.J. (ed.). *Clarendon Press*, Oxford.

Gauthier J., Kluge A.G. & Rowe T., 1988 - Amniote phylogeny and the importance of fossils. *Cladistics*, 4: 105-209.

Gow C.E., 1975- The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana*, 18: 89-131.

Huene F.v., 1944 - Über die systematische Stellung von *Trachelosaurus* aus dem Buntsandstein von Bernburg. *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, Monatshefte*, Abt. B, 1944: 170-174.

Huxley T.H., 1871 - A Manual of the Anatomy of Vertebrated Animals. London.

Jalil N.-E, 1997 - A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. *Journal of Vertebrate Paleontology*, 17: 506-525.

Kearney M., 2002 - Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. *Systematic Biology*, 51: 369-381.

Kearney M. & Clark J.M., 2003 - Problems due to missing data in phylogenetic analyses including fossils: a critical review. *Journal of Vertebrate Paleontology*, 23: 263-274.

Kuhn-Schnyder E., 1954 - Über die Herkunft der Eidechsen. *Endeavour*, 13: 215-221.

Kuhn-Schnyder E., 1974 - Die Triasfauna der Tessiner Kalkalpen. *Vierteljahresschrift der naturforschenden Gesellschaft in Zürich, Neujahrsblatt*, 118: 1-119.

Meyer H.v., 1847-1855 - Zur Fauna der Vorwelt. Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus buntem Sandstein und Keuper. *Heinrich Keller*, Frankfurt a.M.

Meyer H.v., 1856 - Zur Fauna der Vorwelt. Saurier aus dem Kupferschiefer der Zechstein Formation. Frankfurt a.M.

Nopcsa F.v., 1930 - Notizen über *Macrochemus Bassanii* nov. gen. et spec. *Centralblatt für Mineralogie, Geologie und Paläontologie*, B 1930: 252-255.

Nopcsa F., 1931 - *Macrocnemus* nicht *Macrochemus*. *Centralblatt für Mineralogie, Geologie und Paläontologie*, B 1931: 252-255.

Olsen P.E., 1979 - A new aquatic eosuchian from the Newark supergroup (Late Triassic – Early Jurassic) on North Carolina and Virginia. *Postilla*, 176: 1-14.

Olsen P.E. & Sues H.-D., 1986 - Correlation of continental Late Triassic and Early Jurassic sediments and patterns of the Triassic-Jurassic tetrapod transition. In: The Beginning of the Age of Dinosaurs. Faunal Changes across the Triassic – Jurassic Boundary, K. Padian (ed.). *Cambridge University Press*, Cambridge.

Otschev V.G., 1986 - Concerning the Middle Triassic reptiles from the southern Cis-Ural region. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva (Akademia Nauk SSSR, Leningrad)*, 29: 171-179.

Owen R., 1842 - Description of parts of the skeleton and teeth of five species of the genus *Labyrinthodon* (*Lab. leptognathus*, *Lab. pachygnathus* and *Lab. ventricosus*, from the Coton-end and Cubbington Quarries of the Lower Warwick Sandstone; *Lab. Jaegeri*, from Guy's Cliff,Warwick; and *Lab. scutulatus*, from Leamington); with remarks on the probable identity of the *Cheirotherium* with this genus of extinct batrachians. *Transactions of the Geological Society of London*, 6 (2): 515-543.

Parrington F.R., 1935 - On *Prolacerta broomi* gen et sp. n., and the origin of lizards. *Annals and Magazine of Natural History*, 16 (10): 197-205.

Peters D., 2000 - A reexamination of four prolacertiforms with implications for pterosaur phylogenesis. *Rivista Italiana di Paleontologia e Stratigrafia*, 106 (3): 293-336.

Peyer B., 1931 - Die Triasfauna der Tessiner Kalkalpen, II. *Tanystropheus longobardicus* Bass. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 50: 5-110.

Peyer B., 1931b - *Macrocnemus*, nicht *Macrochemus*. *Centralblatt für Mineralogie, Geologie und Paläontologie*, B 1931: 190-192.

Peyer B., 1937 - Die Triasfauna der Tessiner Kalkalpen. XII. *Macrocnemus bassanii* Nopcsa. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft*, 59: 1-140.

Pinna G., 1980 - *Drepanosaurus unguicaudatus*, nuovo genere nuova specie di Lepidosauro del Trias Alpino (Reptilia). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, 121 (3): 181-192.

Pinna G., 1984 - Osteologia di *Drepanosaurus unguicaudatus*, Lepidosauro triassico del Sottordine Lacertilia. *Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano*, 24 (1): 7-28.

Pinna G., 1986 - On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from Italian Alps. *Journal of Palaentology*, 60 (5): 1127-1132.

Pinna G., 1987 - Un nuovo esemplare giovanile di *Drepanosaurus unguicaudatus* del Norico della Val Preone (Udine) (Lacertilia). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, 128 (1-2): 80-84.

Pinna G., 1993 - The norian reptiles of Northern Italy. *Paleontologia Lombarda*, 2: 115-124.

Renesto S., 1994a - The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the Upper Triassic (Norian) of Northern Italy. *Zoological Journal of the Linnean Society*, 111: 247-264.

Renesto S., 1994b - *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of Northern Italy. *Journal of Vertebrate Paleontology*, 14 (1): 38-52.

Renesto S., 1994c - A new prolacertiform reptile from the Late Triassic of Northern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 100: 285-306.

Renesto S., 2000 - Bird-like head on a chameleon body: a new specimen of the enigmatic diapsid reptile *Megalancosaurus* from the Late Triassic of Northern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 106: 157-180.

Renesto S. & Dalla Vecchia F.M., 2000 - The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, Northern Italy). *Journal of Vertebrate Paleontology*, 20 (3): 622-627.

Renesto S., Dalla Vecchia F.M. & Peters D., 2002 - Morphological evidence for bipedalism in the Late Triassic Prolacertiform reptile *Langobardisaurus*. *Senckerbergiana lethaea*, 82 (1): 95-106.

Renesto S. & Paganoni A., 1995 - A new *Drepanosaurus* (Reptilia, Neodiapsida) from the Upper Triassic of Northern Italy. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 97 (1): 87-99.

Robinson P.L., 1975 - The functions of the hooked fifth metatarsal in lepidosaurian reptiles. *Colloques Internationaux C.N.R.S.*, 218: 461-483.

Romer A.S., 1956 - Osteology of the Reptilia. *The University of Chicago Press*, Chicago.

Romer A.S., 1966 - Vertebrate Paleontology, 3rd ed., *The University of Chicago Press*, Chicago.

Romer A.S., 1968 - Notes and Comments on Vertebrate Paleontology. *The University of Chicago Press*, Chicago.

Sanz J.L. & López-Martínez N., 1984 - The prolacertid lepidosaurian *Cosesaurus aviceps* Ellenberger & Villalta, a claimed "protoavian" from the Middle Triassic of Spain. *Geobios*, 17: 747-753.

Sun A., Li J., Ye X., Dong Z. & Hou L., 1992 - The Chinese Fossil Reptiles and Their Kins. *Science Press*, Beijing.

Swofford D. L., 1990 - PAUP - Phylogenetic Analysis Using Parsimony, Version 3.0. *Illinois Natural History Survey*, Champaign.

Swofford D. L. & Begle D.P., 1993 - PAUP - Phylogenetic Analysis Using Parsimony, Version 3.1. *Laboratory of Molecular Systematics, Smithsonian Institution*, Washington DC.

Tatarinov L.P., 1978 - Triassic prolacertilians from the U.S.S.R. *Paleontological Journal*, 12: 505-514.

Thorley J.M. & Page R.D.M., 2000 - RadCon: phylogenetic tree comparison and consensus. *Bioinformatics*, 16: 486-487.

Wild R., 1973 - Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 95: 1-162.

Wild R., 1976 - Neues über den Giraffenhalssaurier *Tanystropheus*. *Natur und Museum*, 106: 13-22.

Wild R., 1980a - Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue Funde von *Tanystropheus* (Reptilia, Squamata). *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 102: 1-31.

Wild R., 1980b - *Tanystropheus* (Reptilia: Squamata) and its importance for stratigraphy. *Mémoires de la Société Géologique de France*, N.S. 139: 201-206.

Young C.-C., 1973 - (*Prolacertoides jimusarensis*). Vertebrata PalAsiatica, 11: 46-48.

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